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1 **Ancestral morphology of crown-group molluscs revealed by a new**
2 **Ordovician stem aculiferan**

3

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17

18 **Exceptionally preserved fossils provide crucial windows on extinct body**
19 **plans and organismal evolution¹. Molluscs, one of the most disparate**
20 **animal phyla, radiated rapidly during the early Cambrian (~535-520 Ma)².**
21 **The problematic fossil taxa *Halkieria*³ and *Orthrozanclus*⁴ (grouped in**
22 **Sachitida) have been assigned variously to stem-group annelids,**
23 **brachiopods^{4,5}, stem-group molluscs⁴ or stem-group aculiferans**
24 **(Polyplacophora + Aplacophora)⁶, but their affinities have remained**
25 **controversial due to a lack of preserved diagnostic characters. Here we**

describe the youngest known sachitid, *Calvapilosa kroegeri* gen. et sp. nov., from the Early Ordovician (~478 Ma) Fezouata biota of Morocco^{7,8}. The new taxon is characterized by the presence of a single large anterior shell plate and a polystichous radula bearing a median tooth and several lateral and uncinal teeth in more than 125 rows. Its flattened body is covered by hollow spinose sclerites, and a smooth, ventral girdle flanks an extensive mantle cavity. Phylogenetic analyses resolve *C. kroegeri* as a stem group aculiferan together with other single plated forms such as *Maikhanella-Siphogonuchites* and *Orthrozanclus*; *Halkieria* is recovered closer to the aculiferan crown. These genera document the stepwise evolution of the aculiferan body plan from forms with a single, almost conchiferan-like shell via two plated taxa such as *Halkieria*, to the eight-plated crown group aculiferans. *C. kroegeri* therefore provides key evidence concerning the long debate about the crown molluscan affinities of sachitids. This new discovery strongly suggests that the possession of only a single calcareous shell plate and the presence of unmineralised sclerites are plesiomorphic for the molluscan crown.

Mollusca Linnaeus, 1758

Sachitida He, 1980

(This clade includes Aculifera plus stem taxa Halkieriidae, *Orthrozanclus*, Siphogonuchitidae)

Siphogonuchitidae Qian, 1977

(This clade contains *Calvapilosa*, *Siphogonuchites*, *Dabashanites*, *Drepanochites*, *Lomasulcachites*, *Lopochites*, *Quadrosiphogonuchites*)

51 ***Calvapilosa kroegeri*** gen. et sp. nov.

52 **LSID.** urn:lsid:zoobank.org:pub:C0C05357-69A2-4937-A28F-C52854CF2870

53 **Etymology.** *Calva* (L), scalp and *pilosus* (L), hairy/shaggy for the head plate

54 covered by densely spiculated mantle. Species named for Björn Kröger for

55 ‘discovering’ the holotype in the collections at Yale.

56

57 **Holotype.** Yale Peabody Museum YPM 237255 (Fig. 1 and Extended Data Fig. 1).

58 **Other material.** Paratypes: YPM 227515 (Fig. 2 a-c, h, j and Extended Data Fig.

59 2), 530835 (Extended Data Fig. 4c), 530836 (Fig. 2d-e and Extended Data Fig. 4c,

60 d, Extended Data Fig. 5d, e) and 530837 (Extended Data Fig. 4a, b and Extended

61 Data Fig. 5a).

62 Other specimens: ?YPM 227641 (Extended Data Fig. 4g, h), 515766.

63 **Locality and horizon.** *Calvapilosa* occurs throughout the classical collecting area

64 of the Fezouata biota to the north of Zagora. The holotype was collected in the

65 Bou Zorgan area. The other specimens were found at additional excavations in

66 this area, near Bni Zoli, in the Bou Glf and Tamagroute areas and on the western

67 flank of Jbel Tigizigzaouine. All localities belong to the Fezouata Formation,

68 *Araneograptus murrayi* graptolite biozone, upper Tremadocian (Lower

69 Ordovician). Detailed locality data are curated with the specimens.

70

71 **Diagnosis for genus and species.** Elongate sachitid-grade aculiferan bearing a

72 single, large subquadratic anterior shell plate with an anteriorly placed mucro.

73 Dense dorsal covering of fine, hollow, spinose sclerites with inconspicuous

74 morphological zonation. Shell plate largely covered by the mantle and sclerites.

75

The single anterior shell plate is subquadratic in outline, the apex (mucro) situated anterior of the mid-length resulting in a steeper anterior than posterior slope (Fig. 2a-b, Extended Data Fig. 4). A shallow concave posterior median indentation in the shell plate of smaller (subadult) individuals (Fig. 1) is subdued into an almost straight margin in larger specimens (Extended Data Fig. 4). The shell plate exhibits holoperipheral growth. Partially infilled structures along the margin may be aesthete canals (Fig. 2a, b, f)⁶. The dorsal surface of the mantle is covered by hollow spinose sclerites, which do not appear to be arranged in distinct morphological zones. If sclerites are present on the ventral surface they are too small to be discerned (<40µm). The ventral mantle is preserved as a smooth brown-stained surface (Fig. 2a, Extended Data Figs 2a-d, 3). The mantle cavity (evident as a ridge in YPM 227515, and a colour difference in YPM 237255) extends along the entire length of the trunk. The radula bears at least 125 tooth rows comprising a median tooth and several flanking teeth (Fig. 2c-e, Extended Data Figs 5, 6a-e). These can be divided into lateral and uncinal teeth using terminology applicable to chitons⁹ (Extended Data Figs 5e, 6a-e), but the exact number is difficult to discern. The median tooth is separated from a major cusp by at least four smaller lateral teeth (Extended Data Figs 5e, 6d). A suite of oblique and posteriorly oriented uncinal teeth lies further abaxially (Extended Data Figs 5e, 6b, c, e).

The position of the radula confirms that the shell plate is anterior. A posterior shell plate, such as that in *Halkieria evangelista*^{3,5} (and likely also *Oikozetes*), is absent (Figs 1, 2 and Extended Data Figs 1, 2): the cover of dorsal sclerites is uninterrupted where such a plate would be situated (Fig. 1).

100 The body of the holotype YPM 237255 (Fig. 1), which is the smallest
101 known specimen, is 16.7mm long and 7.6mm wide, whereas the almost complete
102 YPM 227515 (Fig. 2, Extended Data Fig. 2a-b) is 68.3 mm in preserved length and
103 at least 31 mm wide. Extrapolating from the largest isolated shell plates
104 (Extended Data Fig. 4), individuals reached at least 120 mm in length. Sclerites
105 vary in cross section from polygonal, to square to circular (Fig. 2j). The dorsal
106 sclerites in YPM 227515 are $54\ \mu\text{m} \pm \sim 20\ \mu\text{m}$ in diameter internally, $\sim 70\ \mu\text{m}$
107 externally, and about 0.8 mm long (Fig. 2i-j, Extended Data Fig. 2f-g). Those in
108 the holotype may solely be preserved as diagenetic infills (Extended Data Figs 5,
109 6f-i), and are $57\ \mu\text{m} \pm \sim 20\ \mu\text{m}$ in diameter and vary from 0.5-1.2 mm in length. It
110 therefore appears that the sclerites in the juveniles were larger relative to their
111 body size. An isolated shell (227641) plate differs in details of shape and is therefore
112 only tentatively assigned to *C. kroegeri* (Extended Data Fig. 4g-h).

113 The phylogenetic position of sachitids and wiwaxiids, which have been
114 grouped together into Halwaxiida by some authors⁴, has been a topic of debate.
115 Sachitids have been interpreted as stem brachiopods^{5,10} or basal aculiferan
116 molluscs^{6,11}, while halwaxiids as a whole have been considered to represent
117 either stem molluscs^{4,12}, or the stem group of both brachiopods and annelids⁴
118 (see Supplementary Text). *C. kroegeri* provides new data, which allow the
119 affinities of sachitids and wiwaxiids to be clarified. It possesses a number of
120 unequivocal molluscan synapomorphies identified in sachitids for the first time,
121 including a radula and mantle cavity, together with mineralized sclerites and a
122 shell plate. Such a combination occurs only in aculiferan molluscs (chitons and
123 aplacophorans) among extant taxa. *C. kroegeri* is distinguished from other
124 sachitids by the possession of slender, spinose sclerites and the lack of

conspicuous sclerite zones (distinct sclerite zones may also have been absent in siphogonuchitids¹³). Sclerite morphology and zonation also vary among modern aculiferans⁹.

Our phylogenetic analysis (Fig. 4, Extended Data Figs 8-9; see Supplementary Text and nexus files with character matrices) suggests an evolutionary sequence from Cambrian sachtids, via *C. kroegeri*, towards crown aculiferans. The analysis indicates that a single anterior shell plate was acquired prior to the addition of further shell plates in *Halkieria* and crown group aculiferans. Fossil, morphological and molecular data in a Total Evidence approach¹⁴ suggest that the aculiferan crown group diversified around the Cambrian/Ordovician boundary¹⁵ (Fig. 4, Extended Data Fig. 9). The earliest crown or upper stem aculiferans (e.g. *Matthevia*¹⁵) have an anterior holoperipheral valve followed by seven self-similar mixoperipheral/hemiperipheral valves. Extant chitons maintain the plesiomorphic complement of eight shell plates but this number is reduced, ultimately to zero, in aplacophorans. This loss is heralded by the presence of seven shell plates in the Silurian total group aplacophorans *Acaenoplax*¹⁶ and *Kulindroplax*¹⁷, and echoed in seven serially repeated calcium-secreting papillae in living *Chaetoderma*¹⁸ and seven iterated regions in a neomeniomorph aplacophoran post-larva¹¹. During development, the anterior and intermediate shell plates form first and the posterior shell plate is added later¹⁹. The absence of a holoperipheral posterior shell plate in *Kulindroplax* may indicate that it was lost before the intermediate and anterior shell plates in aplacophorans, and supports the scenario in which aplacophorans evolved through progenetic paedomorphosis²⁰.

150 We recovered the 17-plated multiplacophorans²¹ outside the
151 polyplacophoran crown group, in a similar position to that obtained previously²².
152 Our analyses therefore suggest that the separation of lateral shell plates in
153 Multiplacophora is an autapomorphy that is not related to the origin of the
154 aculiferan or polyplacophoran body plan. The similarities between
155 multiplacophoran shells and those in crown group chitons ^{21,22}, and even in very
156 derived Cretaceous chitons²², suggests convergent evolution.

157 The placement of *C. kroegeri*, *Halkieria* and the other sachitids on the stem
158 of Aculifera, rather than on the molluscan stem, allows us to generate a new
159 hypothesis for the assembly of the molluscan body plan. The ancestral mollusc
160 was previously considered shell-less and aplacophoran-like²³ or showing the
161 eight-fold serialization evident in chitons and the soft tissues of
162 monoplacophorans²⁴. Evidence from molecules, fossils and morphology,
163 however, indicates that the aculiferan morphology is not plesiomorphic—the
164 group is a derived clade and sister taxon to conchiferans²⁵. Aplacophorans lost
165 their shells secondarily – thus the characters shared by polyplacophorans and
166 conchiferans, such as possession of a shell, are plesiomorphic for the mollusc
167 crown group.

168 The presence of multiple muscle scars in monoplacophorans, fossil
169 cephalopods²⁶ and bivalves has been invoked as evidence of a chiton-like
170 ancestor for conchiferans. The phylogenetic position of *C. kroegeri*, however,
171 indicates that a single shell is a synapomorphy of Aculifera as well as Conchifera.
172 This is consistent with the fossil evidence: diverse conchiferans and sachitids
173 appear in the earliest Cambrian (~535 Ma) whereas the first unequivocal
174 multivalved chiton-like fossils are late Cambrian in age (~495 Ma)²⁷. Thus the

evidence suggests that a single shell was present in the molluscan crown ancestor.

C. kroegeri suggests that the ancestral radula comprised a median tooth and several lateral teeth, the heterodontous and polystichous condition found in chitons and several living conchiferans. A comparable morphology is evident in *Odontogriphus* and *Wiwaxia*²⁸ from the Burgess Shale, which we recovered on the molluscan stem (Fig. 4), but the radulae of these taxa are characterized by only 4-6 largely undifferentiated tooth rows. The radula was lost in bivalves and reduced in some aplacophorans such as *Chaetoderma*, which has a single tooth row²⁹.

Aculiferan sclerites are chitinous structures enveloping a calcareous body⁶. The chitinous bristles of chitons and juvenile octopods are probably homologous, and likely represent a synapomorphy of a spiralian subgroup³⁰. Unmineralised chitinous sclerites are also present in wiwaxiids, suggesting that they were also a feature of the ancestral mollusc.

The discovery of a well-preserved radula in an articulated sachitid demonstrates their molluscan affinities and provides a likely answer to the phylogenetic position of these animals. The morphology of *C. kroegeri* provides key evidence informing the stepwise evolution of the aculiferan body plan from a single shelled form, via two shells, to the eight plated chitons and secondarily reduced vermiform aplacophorans. Our new discovery suggests that the last common ancestor of aculiferans and conchiferans possessed a radula with numerous rows of differentiated teeth, non-biomineralised chaetae, and a single calcareous shell. This body plan gave rise to the remarkable morphological

diversity characteristic of the molluscan classes - a disparity that has confounded previous attempts to reconstruct the evolutionary history of the group.

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282

283 **Supplementary information** is available in the online version of the paper.

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 285 and provided support in the field. B. Kröger ‘discovered’ the holotype in 2014
 286 amongst freshly collected and at the time uninventoried material at the Yale Peabody
 287 Museum. L. Ben Moula and B. Tahiri provided practical assistance. S. Butts and J.
 288 Utrup curated specimens and facilitated access to the collections at the YPM. The
 289 drawings of *C. kroegeri* were made by Zubin Dutta and the physical reconstruction
 290 was done by Esben Horn (10tons.dk). The research was supported by National
 291 Science Foundation Grant EAR-1053247 and by the Division of Invertebrate
 292 Paleontology, YPM.

293

294 **Author Contributions** JV initially analysed the fossils and wrote the first
 295 manuscript draft with significant input to both from all other authors. LP and JV

assembled the character matrix. LP did the phylogenetic analyses and produced the interpretative drawings. PVR, JV and LP photographed the fossils. PVR obtained the specimens and locality information through Mohamed ‘Ou Said’ Ben Moula, and prepared the fossils. DEGB facilitated curation and accession of material to YPM.

Author information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and request for materials should be addressed to JV. (jakob.vinther@bristol.ac.uk).

Figure 1 | *Calvapilosa kroegeri*, holotype YPM 237255, from the Lower Ordovician (Tremadocian) Fezouata Formation, near Zagora, Morocco. a, Part; **b**, Interpretative drawing.

Figure 2 | Details and additional specimens of *C. kroegeri*. a, Paratype YPM 227515, part, preserving both dorsal and ventral mantle (Extended Data Fig. 3) in addition to anterior shell. **b**, Radial imprints of putative aesthete canals, arrowed. **c**, Radula. **d**, Radula in YPM 530836, see also Extended Data Fig. 4 and 5. **e**, Detail of (**d**), note the attachment base of a median tooth (arrowed). **f**, Infilled putative radial aesthete canals (arrowed) in YPM 530836. **g**, Sclerites near margin YPM 237255 (Fig. 1). **h**, Sclerites from folded section of dorsal mantle in YPM 227515 (**a** and Extended Data Fig. 2). **i**, SEM detail of sclerites in

longitudinal section in YPM 237255. **j**, Sclerites in cross section in YPM 227515, showing angular external outlines.

Figure 3 | Reconstruction of *Calvapilosa kroegeri*, juvenile. a, Dorsal view. **b**, ventral view. **c**, lateral view. Colour scheme is speculative, while soft tissues are inferred by phylogenetic bracketing. See also Extended data Fig. 7. Resin model constructed by Esben Horn (10tons.dk)

Figure 4 | Time tree of aculiferan evolution based on a Bayesian total evidence analysis. Based on 62 taxa, 134 morphological characters and 2054 amino acid loci analysed in MrBayes. Error bars at nodes are 95% HPD intervals, and the time axis is truncated at the end of the Permian and within the Ediacaran. See Extended data Fig. 8 and 9 and Supplementary Information for details of the phylogenetic analysis. Scale in millions of years before present.

METHODS

No statistical methods were used to predetermine sample size.

The fossils were mechanically prepared using PaleoToolsME9100, PaleoAro, MicroJack5 and MicroJack1 air scribes, and needles and scalpels. Specimens were glued with Paraloid B-72 dissolved in acetone.

Lighting for the overview photographs of dry, uncoated specimens was provided by a Schott KL 1500 fiber optic light source with moveable polarisers fitted at the end of the goosenecks; a Cokin XPro X164 circular polarizer was mounted on the camera lens and crossed with the polarizer of the light source to maximize contrast. All parts were lit from the northwest. Counterparts were illuminated from the southwest and mirrored horizontally in Adobe Photoshop CC 2015.4 to create a

345 false-positive relief image and facilitate direct comparison of part and counterpart.
346 Photographs were taken with a Hasselblad H4D-200MS medium frame digital single-
347 lens reflex camera attached to a computer and operated remotely in six-shot mode
348 through Hasselblad Phocus 8.2.1 software to acquire images of 200 megapixel
349 resolution using a Hasselblad HC Macro 4/120mm II lens stopped down to f/9.5. Lens
350 distortion was corrected using Hasselblad Phocus 8.2.1 software. Stacks of between
351 20 and 50 images were taken in aperture priority mode, with manual focusing through
352 the focal plane. After exporting the FFF-format digital negatives to TIFF from
353 Hasselblad Phocus 8.2.1, the photographs were stacked in Zerene Stacker Pro 1.04
354 Build T201602151850 (64 bit) using the PMax pyramid stack algorithm. The stacked
355 images were then post-processed in Adobe Photoshop CC 2015.4, first applying the
356 ‘Sharpen’ function, followed by removal of the background. Levels were then
357 manually balanced while holding down the ‘alt’ key to prevent clipping of pixels in
358 the specimen; the grey level was always retained at 50%. In a few cases, some minor
359 adjustments were made to the exposure. The high-resolution images were down-
360 sampled in Adobe Photoshop CC 2015.4 to lower resolution TIFF files for use in the
361 plates.

362 Additional photographs were taken with a Nikon d800 using a 105 mm microNikkor
363 lens with or without a 2x teleconverter. Images were taken using a variety of
364 configurations and lighting conditions, including crossed polarised light and normal
365 incident light, in order to highlight different features. Details were imaged under a
366 Leica M60 or M205 C microscope. In some cases, specimens were whitened with
367 ammonium chloride prior to photography to enhance contrast.

368 Specimens were also imaged in a Zeiss Sigma HD VP Field Emission SEM to reveal
369 fine details and preservation of shell plates and sclerites.

A morphological matrix of 62 taxa and 134 morphological characters was analysed using equal and implied weights ($k=3$) parsimony with TNT 1.1 using traditional search options with 10000 replicates. Bayesian analyses of the morphological data utilised MrBayes 3.2.6 and were performed under the Mkv + G model for discrete characters. Total evidence analyses were performed using a modified version of a published molecular dataset¹⁵ consisting of 2054 concatenated amino acids from 7 nuclear house keeping genes with MrBayes 3.2.6 under the uniform tree prior using the IGR clock model, and Mkv + G and LG + I + G for the morphological and molecular partitions respectively. Full details of phylogenetic analyses are included in Supplementary Information.

Data Availability Statement.

Nexus files, containing morphological and molecular sequences used in phylogenetic and total evidence analyses are provided in the online supplementary data. All specimens have been figured in good quality in the extended data figures and are furthermore available in original resolution from the corresponding author.

Extended Data Figure 1 | *Calvapilosa kroegeri* YPM 237255, holotype. a, Part illuminated from north west. **b**, Counterpart, illuminated from south west and then mirrored horizontally. **c**, Part, submerged in water.

Extended Data Figure 2 | *Calvapilosa kroegeri* YPM 227515, paratype. a, Part, illuminated from north west. **b**, Counterpart, illuminated from south west and then mirrored horizontally. **c**, Interpretative drawing of YPM 227515 part and counterpart combined. Interpretations below the stippled line are derived

from the counterpart. Boxes denote position of details. Areas shown in green are of exposed ventral mantle, areas within dashed lines denote gaps in preservation, darker blue shows the teeth of the radula and lighter blue denotes the shell. Sclerites are shown in orange but are only drawn where lying flat or covering the shell. **d**, Exposed ventral mantle, which is preserved in darker colouration but shows no visible sclerites. **e**, Folded dorsal mantle which preserves dorsal sclerites in longitudinal section. **f**, Dorsal sclerites. **g**, Dorsal sclerites in cross-section and marginal sclerites in longitudinal section.

Extended Data Figure 3 | Cartoon explaining preservation of YPM 227515, cross-sectional view. a, Prior to burial. **b**, Burial. **c**, Decay and replacement of the mantle and sclerites by pyrite. **d**, Compaction. **e**, Weathering and uneven splitting along the dorsal mantle, cross cutting sclerites and along smooth, ventral mantle.

Extended Data Figure 4 | Additional specimens of *C. kroegeri* and *Calvopilosa* sp. a, YPM 530837, isolated head valve with radula preserved. **b**, counterpart, mirrored. **c**, YPM 530836, isolated head valve with radula preserved. **d**, counterpart, mirrored. **e**, YPM 530835, isolated head valve. **f**, counterpart, mirrored. **g**, YPM 227641, *Calvopilosa ?kroegeri*. isolated head. **h**, counterpart, mirrored.

Extended Data Figure 5 | The radula of *C. kroegeri*. a, YPM 530837. **b**, YPM 227515. **c**, YPM 237255. **d**, YPM 530836. **e** and **f**, detail of (**d**) with explanatory drawing showing basal attachment points of radula teeth. Labels denote: Ur,

uncinal region; Mc, major cusp; La, lateral area; Mt, median tooth. Stippled areas obscured by overlying mineral.

Extended Data Figure 6 | SEM images of *C. kroegeri* sclerites and radula. a, YPM 530836 indicating regions from which SEM photomicrographs b-e were obtained. **b,** left major cusps and adjacent uncinal teeth. **c,** left uncinal region. **d,** overview showing median teeth (a single tooth indicated by white arrow), broad flanking region with lateral teeth (a single tooth indicated by black arrow) and major cusps. **e,** right uncinal teeth. **f,** YPM 237255 indicating where SEM photomicrographs g-i were obtained. **g,** sclerites with diagenetic infill. **h,** sclerites in longitudinal section. **i,** sclerite in longitudinal section preserved as a void. b-h and g-i were taken using backscatter and secondary electron imaging respectively.

Extended Data Figure 7 | Reconstruction of *C. kroegeri*. a, juvenile. **b,** adult dorsal view. **c,** adult lateral view. **d,** adult ventral view. Drawing by Zubin Dutta.

Extended Data Figure 8 | Morphological phylogenetic analyses of molluscs incorporating *C. kroegeri*. a, strict consensus of 369 trees of length 209 from parsimony analysis under equal character weighting, numbers at nodes are from 1000 bootstrap replicates, 1000 Jackknife replicates and Bremer support respectively. **b,** parsimony analysis under implied weighting ($k=3$), numbers at nodes are from 1000 replicates of symmetric resampling. **c,** Results of Bayesian analysis using the $mkv + \Gamma$ morphology model, numbers at nodes are posterior probabilities.

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446 **Extended Data Figure 9 | Bayesian Total evidence dating analysis**

447 **incorporating *C. kroegeri*.** Analysis performed using the uniform tree prior and

448 LG + Γ and *mkv* + Γ for the molecular and morphological data respectively. The

449 topology shown is for analysis using a 549Ma maximum on the age of the

450 molluscan crown group. Error bars on node ages are 95% HPD intervals for both

451 unconstrained analyses (red) and analyses with the maximum age constraint on






452 molluscs (purple). Numbers at nodes are posterior probabilities from the

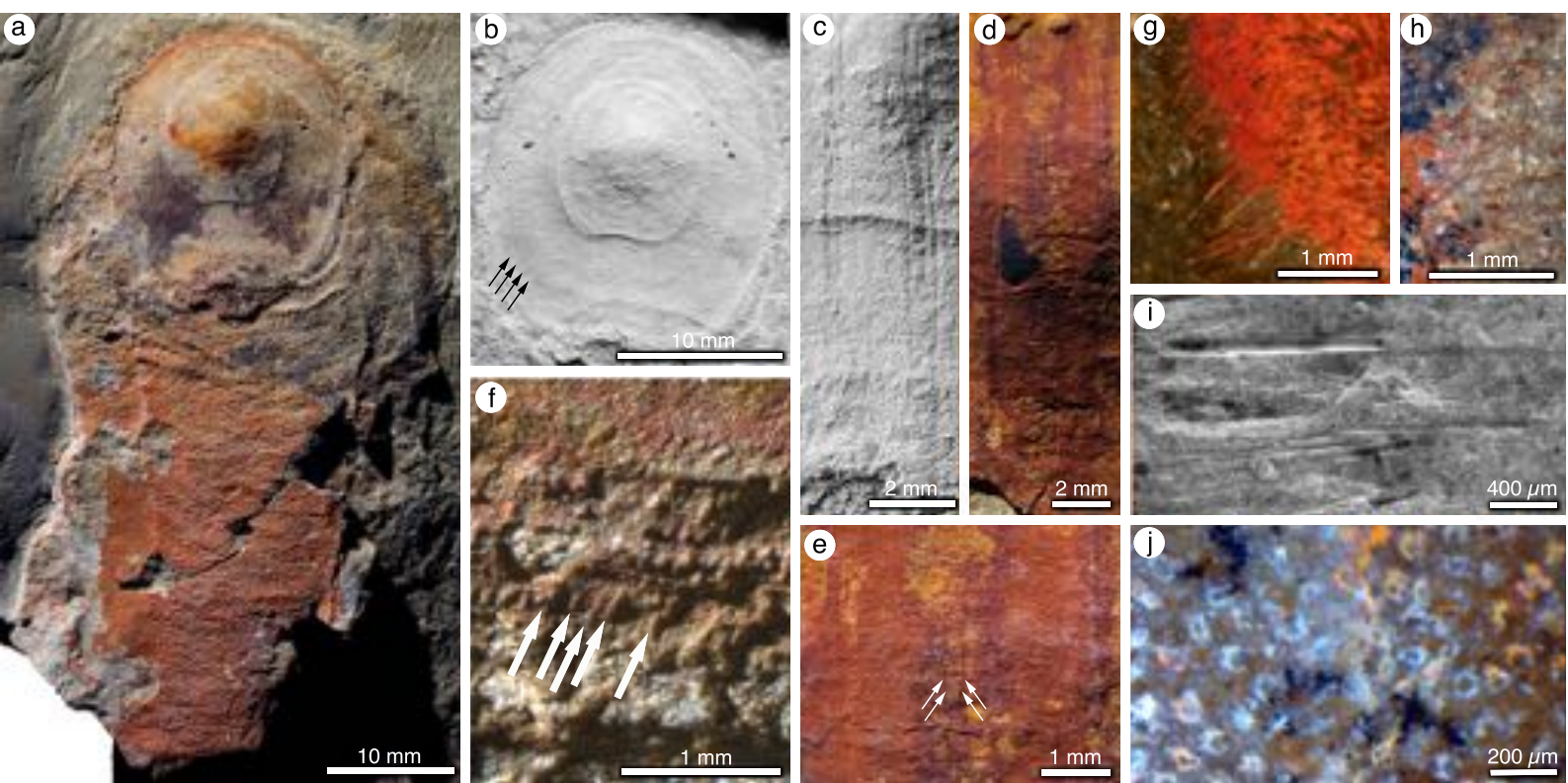
453 constrained analysis.

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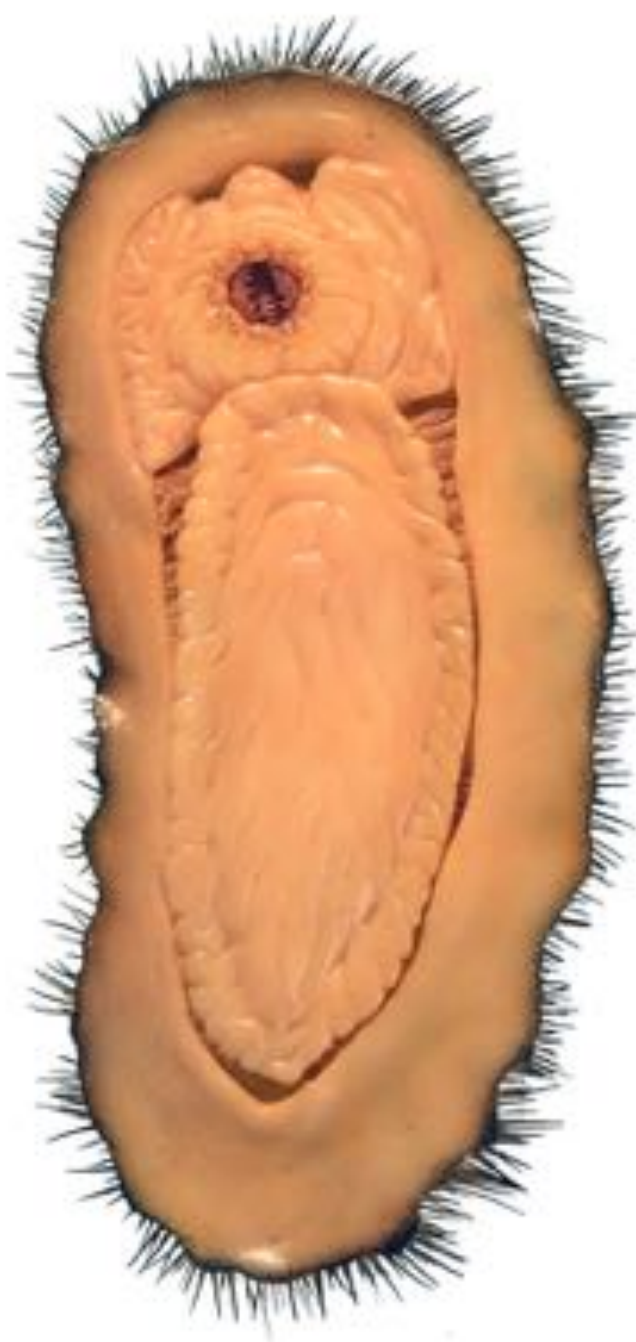
- | | | |
|---|---|--|
|  Sclerites |  Mantle cavity/foot region | |
|  Exposed shell area |  Dorsal mantle |  Radula |



a



b



c



